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The Red Algal Genus  
*Audouinella* Bory  
(Nemaliales: Acrochaetiaceae)  
from North Carolina

CRAIG W. SCHNEIDER



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The Red Algal Genus *Audouinella* Bory  
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*Craig W. Schneider*

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## ABSTRACT

Schneider, Craig W. The Red Algal Genus *Audouinella* Bory (Nemaliales: Acrochaetiaceae) from North Carolina. *Smithsonian Contributions to the Marine Sciences*, number 22, 25 pages, 3 figures, 1983.—A monographic study of *Audouinella* in the Atlantic waters of North Carolina reports 15 taxa from coastal and continental shelf habitats. Three of these, *A. affinis*, *A. hoytii*, and *A. ophioglossa*, herein described as a new species, are endemic. *Audouinella bispora* and *A. daviesii* are reported from the Carolina flora for the first time. The taxonomy from several historical reports is elucidated, and taxonomic confusions in this complex are clarified.

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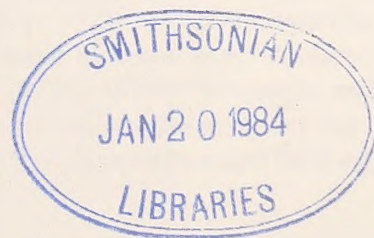
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# The Red Algal Genus *Audouinella* Bory (Nemaliales: Acrochaetiaceae) from North Carolina

*Craig W. Schneider*

## Introduction

The Acrochaetiaceae has received a great deal of systematic attention in the last half century (Drew, 1928; Hamel, 1928b; Papenfuss, 1945, 1947; Abbott, 1962, 1968; Feldmann, 1962; Woelkerling, 1971, 1972, 1973a, 1973b; Dixon and Irvine, 1977; Garbary, 1978, 1979). Nevertheless, many of the species reported or described from North Carolina have received little or no attention since their early notation here (Howe and Hoyt, 1916; Hoyt, 1920; Williams, 1948, 1951). The only taxa updated in a recent systematic listing for North Carolina (Searles and Schneider, 1978) were those species taxonomically treated in other floras. Therefore, the North Carolina checklist contained both recent and antiquated taxonomy in this family, as well as several unsubstantiated reports. This monograph was undertaken to verify and update the taxonomic record. In the process of this work additional taxa have been discovered in the North Carolina flora.

Several genera have been described in Acrochaetiaceae and species have been variously assigned to them on the basis of chromoplast morphology and presence or absence of sexual reproduction (for example, see Garbary, 1979). Because

generic concepts vary from study to study and because frequently utilized generic characters have proved unreliable (Woelkerling, 1971, 1973b), I find that it is more pragmatic and less confusing to follow the single-genus concept for the Acrochaetiaceae previously utilized by Børgesen (1915) and first argued for by Drew (1928). This approach has recently been followed by Dixon and Irvine (1977) and Garbary (1979). The genus with historical precedence is *Audouinella* Bory (1823:340), and its usage requires some new nomenclatural combinations herein proposed. With the advent of further culture work in this family, it is possible that in the future we will be able to resegment the species into more than one genus based on more reliable characters, such as life history characteristics (West, 1968, 1969; Stegenga, 1978; Stegenga and van Wissen, 1979).

Generic confusion aside, species concepts have of late also come under more critical examination. Several a priori standard specific characters such as mode of attachment and reproductive state have been criticized as taxonomic criteria (Borsje, 1973; Stegenga and Borsje, 1976, 1977; Stegenga and Vroman, 1976; Stegenga and Mulder, 1979; Stegenga and van Erp, 1979). Broad circumscriptions of species utilized by some (e.g., Woelkerling, 1971, 1972, 1973a, 1973b; Stegenga and Vroman, 1976) are not universally accepted (e.g., Dixon and Irvine, 1977; Kornmann and Sahling,

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1978; Humm, 1979). The cultural experiments of Stegenga and his associates have paired "distinct" species as heteromorphic generations of one taxon in this family. For the present, however, I continue to follow Woelkerling's classical interpretation of species concepts within *Audouinella* until a more complete understanding of species based upon life history and other features can be synthesized. Included in the scheme listed below, for example, is *Audouinella dasyae*, which is probably a gametophytic generation of either *A. saviana*, *A. hypneae*, or *A. bispora*, or possibly, all of them (Stegenga and Borsje, 1976). One of the asexual taxa mentioned below could possibly be the sporophytic generation of *Scinaia complanata* (Collins) Cotton (van den Hoek and Cortel-Breeman, 1970), though that remains to be determined.

**MATERIALS AND METHODS.**—Where possible, observations, measurements, and drawings were made using living field-collected material or liquid-preserved material. Dried specimens were wetted and removed from herbarium sheets using 10% aqueous sodium carbonate. Permanent slides were produced by either mounting the specimens in 20% Karo syrup, 1% aniline blue, 1 N HCl, 3%–4% formalin in a ratio of 95:1:2:2, or by staining with 1% aniline blue, fixing with 1% HCl, and mounting in 20% Karo with phenol added as a preservative. Drawings were made using a Zeiss camera lucida. Aside from those listed below for DUKE and US, duplicates of some of the author's collection numbers have

been deposited in AHFH, GALW, HBFH, MASS, MICH, NCU, NFLD, NHA, and WNC. Herbarium abbreviations follow Holmgren et al. (1981). Specimen measurements are accurate to 0.1 micrometer.

**ACKNOWLEDGMENTS.**—I thank Duke University for space and assistance at the Marine Laboratory and Dr. W. Kirby-Smith of the Reference Museum for sponsoring an offshore collecting trip and allowing access to the collections. I acknowledge the Duke University Cooperative Program in Oceanography as some of my earlier collections were made on R/V *Eastward* cruises. I also thank fellow scientists (and the herbaria with which they are associated): Drs. R.B. Searles (DUKE), J.N. Norris (US), and D.F. Kapraun (WNC) for loans; Dr. L.G. Williams for sending specimens; and the Duke University Botany Department for access to that herbarium. Dr. M.H. Hommersand assisted with the literature and Dr. J.S. Ramus allowed use of his personal library. Ginny Schneider deserves special thanks for typing during my leave. Drs. Searles, Norris, and W.J. Woelkerling kindly reviewed the manuscript. This research was sponsored by Trinity College as a sabbatical leave.

This monograph is dedicated to the memory of Dr. G.F. Papenfuss, both for his early work with the *Audouinella* complex and for his recent encouragement for me to unravel the taxa in North Carolina.

## Genus *Audouinella*

### Key to the Species of *Audouinella* from North Carolina<sup>1</sup>

(Species alphabetically arranged in text)

1. Plants attached to the substrate by an obvious, persistent, undivided basal spore which may give rise to one or several accessory cells, an endophytic

<sup>1</sup> Several specimens from a population should be observed when utilizing the above key. Some characters, such as presence or absence of unicellular hairs, are variable and by themselves are not considered to be taxonomically significant. In practice, however, a combination of several characters, some apparently more stable than others, is useful in delineating taxa. This key reflects distinctions found in North Carolina specimens; it should also be helpful in distinguishing these "purported" taxa elsewhere.



- branched filament, or a prostrate filamentous system ..... 2
- Plants attached to the substrate by a multicellular prostrate system, the basal spore once septate and persistent, or not obvious, obscured by divisions in the earliest stages ..... 8
- 2. Plants minute, less than 250  $\mu\text{m}$  tall ..... ***A. microscopica***
- Plants larger, greater than 500  $\mu\text{m}$  tall ..... 3
- 3. Basal spores consistently globose or subglobose, obviously larger than erect filaments ..... 4
- Basal spore ovoid to panduriform, globose or subglobose, the same size or only a few micrometers larger than erect filaments ..... 7
- 4. Basal spore producing a single penetrating endophytic branched filament in addition to one or more erect filaments ..... 5
- Basal spore remaining undivided or occasionally producing a few accessory cells ..... 6
- 5. Basal spore 12–15  $\mu\text{m}$  diam., erect filaments 8–13  $\mu\text{m}$  diam.; dioecious, spermatangia forming corymbose clusters on lateral branches ..... ***A. corymbifera***
- Basal spore 7.5–12.5  $\mu\text{m}$  diam., erect filaments 3–5  $\mu\text{m}$  diam.; monoecious, spermatangia paired, produced on opposite or whorled branches in a long series ..... ***A. ophioglossa***
- 6. Monosporangia 5.0–7.5  $\mu\text{m}$  diam., 11–15  $\mu\text{m}$  long ..... ***A. hoytii***
- Monosporangia 10–18  $\mu\text{m}$  diam., 18–27  $\mu\text{m}$  long ..... ***A. affinis***
- 7. Basal spore remaining undivided, ovoid, elongate to rectangular, occasionally with a flared disciform base ..... ***A. hallandica***
- Basal spore, pyriform to panduriform, producing a prostrate filamentous system ..... ***A. dasyae***
- 8. Plants mostly endophytic or endozoic, upright axes less than 150  $\mu\text{m}$  tall ..... ***A. infestans***
- Plants mostly epiphytic, epizoic, or saxicolous, upright axes greater than 200  $\mu\text{m}$  tall ..... 9
- 9. Plastids with more than one pyrenoid per cell ..... ***A. botryocarpa***
- Plastids with only one pyrenoid per cell ..... 10
- 10. Sporangia, for the most part, borne in clusters of 3 or more on branched stalks at the base of lateral branches ..... ***A. daviesii***
- Sporangia, for the most part, borne singly or in pairs, not clustered at the base of lateral branches ..... 11
- 11. Monosporangia 9–13  $\mu\text{m}$  long ..... 12
- Monosporangia 15–40  $\mu\text{m}$  long ..... 14
- 12. Monosporangia 5–6  $\mu\text{m}$  diam.; bisporangia, if present, 7–12  $\mu\text{m}$  diam., 12–18  $\mu\text{m}$  long ..... ***A. bisporea***
- Monosporangia 6–10  $\mu\text{m}$  diam.; bisporangia not present ..... 13
- 13. Plants producing only single monosporangia, erect filaments to 1 mm tall arising from a uniseriate prostrate filament to small compact pseudoparenchymatous disc ..... ***A. hypneae***
- Plants producing single or 2–3 seriate monosporangia, erect filaments to 0.5 mm tall arising from a wide-spreading, much-branched prostrate system, often with a persistent septate basal spore ..... ***A. densa***



14. Plastids stellate, parietal or axial, unicellular hairs common but not present on all plants, plants arising from an orbicular pseudoparenchymatous disc that is often later obscured by proliferating filaments ..... *A. secundata*
- Plastids lobate, parietal or axial, unicellular hairs absent or rare, but terminal cells occasionally taper sharply to the tips, plants not arising from an orbicular pseudoparenchymatous disc in early stages ..... 15
15. Prostrate system a widespreading mass of uniseriate filaments from an enlarged central pyriform to panduriform cell that is persistent but often obscured in older plants, uniseriate prostrate filaments giving rise to numerous erect filaments ..... *A. dasyae*
- Prostrate system a compact, often penetrating mass of uniseriate filaments, usually coalesced centrally to form a pseudoparenchymatous disc, basal spore not persistent ..... *A. saviana*

***Audouinella affinis* (Howe and Hoyt),  
new combination**

FIGURE 1a,b

*Acrochaetium affine* Howe and Hoyt, 1916:118, pl. 15.—Hoyt, 1920:471, pl. 69.—Searles and Schneider, 1978:100.

*Audouinella alariae* sensu Kapraun, 1980:40, figs. 15–17. [Not (Jonsson) Woelkerling, 1973b:541, figs. 1–9.]

**DESCRIPTION.**—Plants epiphytic or epiendo-phytic, to 4 mm tall, caespitose, arising from a persistent, large, globose to subglobose spore, 14–26  $\mu\text{m}$  diam. including an obvious wall 2.5–5.0  $\mu\text{m}$  thick, one half again as big as the cells which emanate from it; if embedded in host tissue, the spore becoming vertically elongate to subpyriform or panduriform, if not, producing a subcylindric obtuse or truncate foot that penetrates to 24  $\mu\text{m}$ , the extended spore 20–33  $\mu\text{m}$  high; spore usually remaining simple, occasionally developing a few smaller accessory cells, rarely producing short prostrate irregularly branched filaments up to 5 cells long; basal spore, and occasionally accessory cells or basal filament cells, producing 1–4 erect filaments, cells cylindrical, 5–14  $\mu\text{m}$  diam., 17–78  $\mu\text{m}$  long, each with a parietal lobate plastid and one pyrenoid; for the most part plants immediately branched from the distal end of the first cell of the erect filament, branching subdichotomous or subtrichotomous, appearing rigid below, more flexuous above, branching mostly subdichotomous to distinctly lateral, ultimate

branches elongate-irrigate, 3.0–5.5  $\mu\text{m}$  diam., gradually tapering toward the apices, often terminating with inconspicuous hairs.

Monosporangia infrequent, lateral, second, or less commonly terminal on upper portions of the plant, sessile or on one-celled pedicels, ovoid, obovoid, or oblong, 10–18  $\mu\text{m}$  diam., 18–27  $\mu\text{m}$  long, occasionally on gametophytic plants. Monoecious, spermatangia in proximity to sessile carpogonia, lateral or terminal, sessile or pedicellate, solitary or in groups of 2 or 3; carposporophytes common, 3–12 spored, carpospores 8–25  $\mu\text{m}$  diam., 13–28  $\mu\text{m}$  long.

**TYPE-LOCALITY.**—Onslow Bay, North Carolina, USA.

**HOLOTYPE.**—US 56005.

**DISTRIBUTION.**—Endemic to North Carolina, as far as currently known.

**NORTH CAROLINA SPECIMENS STUDIED.**—Onslow Bay, reef, 11 Aug 1914, *Radcliffe* (Holotype, US 56005; Isotypes, US 33567, 33584, 33646; Isotypes, DUKE 111, 1458). Beaufort, Radio Is. jetty, 5 Jul 1960, *Aziz* (DUKE 109). Cape Lookout jetty, 23 Jul 1961, *Aziz* (DUKE 102, 108). Beaufort, Radio Is. jetty, 4 Aug 1961, *Aziz* (DUKE 103–107, 110, 120, 121). Onslow Bay, reef, 2 Aug 1971, *Searles* (DUKE 13190). Onslow Bay, reef, 20 Jul 1973, *Schneider 718* (DUKE 12606, 12716; US 50776; CWS). Onslow Bay, reef, 11 Aug 1981, *Schneider 2711* (DUKE 16525; US 88906; CWS). Beaufort, Radio Is. jetty, 20



Jul. 1982, *Schneider* 2867 (CWS).

REMARKS.—This species is an obvious epiphyte of *Dictyota*, *Sargassum*, and other algae from deep (to 30 m) offshore and from shallow subtidal habitats in the Beaufort and Wilmington areas, at times turning the host alga red with a complete or marginal covering of its fine red filaments. To date, found from June to August.

Hoyt (1920) listed several morphological characters useful in distinguishing *Audouinella affinis* from the earlier described *A. hoytii*. Although they are generally helpful, I find the size of monosporangia as the most reliable in the separation of these two closely allied taxa. *A. affinis* appears related to *A. alariae* (Jonsson) Woelkerling (1973b), but can be distinguished by the production of accessory cells from the basal spore and the larger monosporangia. A comparison of type material is needed to clarify the limits of species with persistent globose basal spores.

### *Audouinella bispora* (Børgesen) Garbary

FIGURE 1c-f

*Audouinella bispora* (Børgesen) Garbary, 1979:490.

*Chantransia bispora* Børgesen, 1910:178, fig. 1.

DESCRIPTION.—Plants epiendophytic to 1.5 mm tall, arising from an irregularly ramified, spreading prostrate system that remains superficial or penetrates host tissue, prostrate cells cylindrical to irregular, to 17.5  $\mu\text{m}$  in greatest dimension, all capable of producing an erect filament; erect filaments radially to irregularly branched and rebranched, infrequent below, more above, the branches sharply to narrowly angled from the axes that bear them, tapering toward the apices; cells cylindrical, 2.5–8.0  $\mu\text{m}$  diam., 10.0–32.5  $\mu\text{m}$  long in the main axes, 1.0–3.0  $\mu\text{m}$  diam., in the ultimate segments, occasionally ending in long multicellular, lightly pigmented hair-like extensions, unicellular hairs unknown; each cell containing a well-developed parietal plastid with a single large pyrenoid.

Monosporangia terminal or lateral on short branches to adaxial on longer axes, sessile or on one-celled pedicels, single or paired, narrow,

ovoid to oblong, 5–6  $\mu\text{m}$  diam., 9.5–12.5  $\mu\text{m}$  long; bisporangia situated as monosporangia, single or paired, broad, ovoid to ellipsoidal, 7.5–11.5  $\mu\text{m}$  diam., 12.5–17.5  $\mu\text{m}$  long. Gametangia unknown.

TYPE-LOCALITY.—St. Thomas, Virgin Islands.

HOLOTYPE.—C.

DISTRIBUTION.—North Carolina, St. Thomas (Virgin Islands).

NORTH CAROLINA SPECIMENS STUDIED.—Onslow Bay, reef, 30 June 1972, *Searles* (DUKE 16526). Onslow Bay, reef, 5 May 1981, *Handsel*, BLM 65818086 (Duke Marine Lab Reference Museum).

REMARKS.—Collected to date from water 25–30 m deep in Onslow Bay, May–June. This is the first report of this taxon outside the type-locality. The North Carolina specimens perfectly fit the descriptions of Børgesen (1910, 1915), and I do not hesitate to place them under *Audouinella bispora*. The questions raised by Børgesen (1915) as to whether this plant is indeed a form of *Audouinella hypneae* (Børgesen) Schneider cannot be ascertained without additional comparative material of the latter named species (see discussion of *A. hypneae*). *Audouinella bispora* occasionally produces bispores and has narrower monospores than reported for *A. hypneae*, a feature also seen in North Carolina plants. Nevertheless, it is interesting to note that in Garbary's (1979) cluster analysis, *A. bispora* was found to be quite similar to *A. seriata* (Børgesen) Garbary, a species I consider a synonym of *A. hypneae* in this paper. *Audouinella hypneae* was not treated by Garbary (1979).

The description of *Audouinella bispora* by Børgesen is broadened here based on the variation seen within North Carolina plants, but no characteristics were found that contradict the earlier descriptions.

### *Audouinella botryocarpa* (Harvey) Woelkerling

FIGURES 1g-l

*Audouinella botryocarpa* (Harvey) Woelkerling, 1971:37.—

Searles and Schneider, 1978:100.

*Callithamnion botryocarpum* Harvey, 1854:563.

DESCRIPTION.—Plants epiphytic, epiendophytic



or saxicolous to 1 cm tall, caespitose, arising from an irregularly branched prostrate system with entangled filaments free from one another or coalesced into a pseudoparenchymatous disc, occasionally supplemented by corticating rhizoids descending cells or lower portions of erect filaments; base giving rise to several erect filaments, much and irregularly to unilaterally branched, sometimes terminating abruptly in multicellular hair-like extensions or gradually tapering toward the tips; cells of main axes cylindrical (10–)15–20(–30)  $\mu\text{m}$  diam., 30–120  $\mu\text{m}$  long and 6–15  $\mu\text{m}$  diam. in the ultimate segments, each cell containing a single parietal lobate plastid with one to several pyrenoids, unicellular hairs unknown.

Monosporangia terminal on short branches and adaxial, near the bases of branches, secund or scattered, sessile or on one-celled pedicels, single, paired, or rarely in groups of 3 to 5, ovoid, 12–28  $\mu\text{m}$  diam., 18–43  $\mu\text{m}$  long; tetrasporangia cruciate, with range of dimensions, shape, and position similar to monosporangia, in general somewhat larger than monosporangia on the same plant. Sexual plants unknown in the Carolinas.

TYPE-LOCALITY.—King George's Sound, western Australia.

HOLOTYPE.—*Harvey 324*, travelling collection; not in TCD.

DISTRIBUTION.—North Carolina, Australia, New Zealand.

NORTH CAROLINA SPECIMENS STUDIED.—Beaufort, Radio Is. jetty, 2 Mar 1974, *Schneider 829* (DUKE 13250, 13251, 13264; CWS). Beaufort, Radio Is. jetty, 16 Feb 1975, *Searles 75-1-1* (DUKE 14178; CWS). Beaufort, Radio Is. jetty, 14 Sep 1981, *Schneider 2720* (DUKE 16524; CWS). Beaufort, Pivers Is. seawall, 10 Nov 1981, *Schneider 2746* (DUKE 16590; US 88908; CWS). Beaufort, Pivers Is. seawall, 7–8 Dec 1981, *Schneider 2753* (DUKE; US 88909; CWS). Beaufort, Radio Is. jetty, 20 Jul 1982, *Schneider 2864* (DUKE; US 88910; CWS).

REMARKS.—Known only as an obvious epiphyte of *Codium* from the Pivers Island seawall and Radio Island jetty, Beaufort, but probably more widespread. Collected July–March.

This taxon is at present known in the Atlantic Ocean only from North Carolina and also represents the only member of the acrochaetoid complex with more than one pyrenoid per cell (Figure 1g) from the east coast of North America (Searles and Schneider, 1978). Specimens have been compared with type material by W.J. Woelkerling.

The only plants thus far collected in North Carolina are tetrasporic and/or monosporangiate. Monosporangia, found in all collections, are large, falling in the upper size ranges of those listed by Woelkerling (1970, 1971). Many of the monosporangia are terminal on short branches, some later becoming subtended by the short lateral filaments that produce them, becoming displaced to a lateral position. Later the monosporangia are seen as clustered near the base of branches, presumably due to the subtended filaments forming beneath monosporangia. Tetrasporangia have been found only in December collections. Plants from New Zealand and Australia are no longer than 6 mm, while those in the Carolina region reach 1 cm, by far the largest of the acrochaetoids from this area. Multicellular hair-like extensions have thus far been observed only from the September Radio Island populations; none of these minor differences warrants a separation from the taxon previously known only from the Southern Hemisphere, *Audouinella botryocarpa*.

### *Audouinella corymbifera* (Thuret) Dixon

*Audouinella corymbifera* (Thuret in Le Jolis) Dixon in Parke and Dixon, 1976:590.

*Chantransia corymbifera* Thuret in Le Jolis, 1863:107 [in part].

*Acrochaetium corymbiferum* (Thuret in Le Jolis) Batters, 1902:59.—Hoyt, 1920:473.

*Acrochaetium bornetii* Papenfuss, 1945:313.—Searles and Schneider, 1978:100.

DESCRIPTION.—Plants epiphytic, 2–3 mm tall, arising from a persistent, large, globose spore, 12–15  $\mu\text{m}$  diam., which produces an irregular, contorted branched filament that deeply penetrates host tissue with cells 8–13  $\mu\text{m}$  diam., 25–40  $\mu\text{m}$  long; basal spore and occasional cells of the internal filament giving rise to erect branched axes, secund to alternate with branches more



abundant above and not often rebranched; cells of erect filaments cylindrical, 7–16  $\mu\text{m}$  diam., 22–55  $\mu\text{m}$  long, each cell containing a well-developed parietal lobed plastid with a single pyrenoid, unicellular hairs unknown.

Monosporangia terminal on short branches or lateral, near the bases of branches, sessile or on one-celled pedicels, single, ovoid, 8–10  $\mu\text{m}$  diam., 15–18  $\mu\text{m}$  long, occasionally associated with gametangia. Dioecious, spermatangia lateral on main axes, formed in a corymbose cluster on a 1–2 celled pedicel, colorless, 4–5  $\mu\text{m}$  diam.; carpogonia lateral on a main axis, on a 1–2 celled pedicel near the bases of branches, producing a corymbose carposporophyte with terminal carposporangia, ovoid, 9–15  $\mu\text{m}$  diam., 14–18  $\mu\text{m}$  long.

TYPE-LOCALITY.—Belle-Île-en-Mer, Atlantic France.

HOLOTYPE.—Cannot be located (Dixon and Irvine, 1977:88).

DISTRIBUTION.—North Carolina, Bermuda, Mediterranean, England, France.

NORTH CAROLINA SPECIMENS STUDIED.—Beaufort harbor, 20 May 1907, *Hoyt* (DUKE 135; US 33648).

REMARKS.—Abundant sexually reproductive plants found on one specimen of *Dasya* from Beaufort harbor, to date collected only once, in May.

For a clarification of the correct epithet refer to Dixon and Irvine (1977).

### *Audouinella dasyae* (Collins) Woelkerling

FIGURE 1m–p

*Audouinella dasyae* (Collins) Woelkerling, 1973b:545, figs. 10–31.—Searles and Schneider, 1978:100.—Kapraun, 1980:40 [in part].

*Acrochaetium dasyae* Collins, 1906:191.—Aziz, 1967:408.

*Acrochaetium robustum* sensu Williams, 1948:690; 1951:153.—Taylor, 1960:315 [in part]. [?Not Børgesen, 1915:40, figs. 38–40.]

DESCRIPTION.—Plants epiphytic, to 3 mm tall, caespitose, arising from a basal spore and wide-spreading uniseriate, prostrate filamentous axis it produces; original spore elongated pyriform to

panduriform, not greater in size than the cells which it produces, rarely remaining simple, often becoming obscured by descending rhizoids and entangled prostrate filamentous axes; creeping prostrate system giving rise to several erect filamentous, moderate to much and irregularly branched, often tapering to the tips, cells cylindrical, 6–12(–16)  $\mu\text{m}$  diam., 25–70(–90)  $\mu\text{m}$  long in lower portions, 6–10  $\mu\text{m}$  diam., 15–60  $\mu\text{m}$  long in the ultimate segments, each having a single parietal plastid with one pyrenoid, hairs unknown.

Monosporangia mostly single, occasionally in pairs, secund to scattered, sessile or on one-celled pedicels, ovoid, 7–12(–16)  $\mu\text{m}$  diam., 16–27  $\mu\text{m}$  long, borne on vegetative or gamete-producing plants. Monoecious or dioecious, spermatangia terminal or lateral on specialized short lateral branched axes, globose to ovoid, 2–4  $\mu\text{m}$  diam., 3–5  $\mu\text{m}$  long; carpogonia scattered, sessile or stalked; carposporophytes with numerous terminal and lateral ovoid carposporangia, 9–12  $\mu\text{m}$  diam., 16–24  $\mu\text{m}$  long.

TYPE-LOCALITY.—Woods Hole, Massachusetts, USA.

HOLOTYPE.—FH.

DISTRIBUTION.—Florida to Prince Edward Island (discontinuous; not reported from South Carolina and Georgia).

NORTH CAROLINA SPECIMENS STUDIED.—Cape Lookout jetty, 16 Jun 1947, *Williams* (CWS). Cape Lookout jetty, 14 Aug 1962, *Aziz* (DUKE 125). Beaufort, Pivers Is., 6 Apr 1963, *Aziz* (DUKE 158). Onslow Bay, reef, 16 Jul 1968, *Searles* (CWS). Beaufort, Radio Is. jetty, 8 May 1971, *Schneider 172a* (CWS). Onslow Bay, reef, 11 Aug 1981, *Schneider 2687* (DUKE 16523; CWS).

REMARKS.—Epiphytic on *Dasya*, *Sargassum*, and other hosts from shallow and deep subtidal environments, April–August in the area.

After an examination of Williams's collections of *Acrochaetium robustum*, I find those specimens easily fall within the circumscription of *Audouinella dasyae* (Woelkerling, 1973b); any slight variation in their holdfasts is probably due to the differences in surface textures of the host plants. An examination of Collins type material of *A. robustum*



*tum* is necessary to test whether the two taxa are indeed conspecific. Stegenga and Borsje (1976) have found that *A. dasyae* alternates with a heteromorphic tetrasporophyte provisionally identified as *A. saviana*; however, they felt it premature to deal with the nomenclatural problems arising from their study.

North Carolina plants are often found with an early formed basal system of the ovoid to pyriform spore and one smaller accessory cell from which an upright filament rises obliquely (Figure 1*m,n*).

### ***Audouinella daviesii* (Dillwyn) Woelkerling**

FIGURE 2*a-c*

*Audouinella daviesii* (Dillwyn) Woelkerling, 1971:28, figs. 7, 22.

*Conserva daviesii* Dillwyn, 1809:73, suppl., pl. F.

*Audouinella hallandica* sensu Kapraun, 1980:41, fig. 26 [in part]. [Not *Audouinella hallandica* (Kyllin) Woelkerling, 1973a:82.]

**DESCRIPTION.**—Plants epiphytic, epiendophytic, epizoid, or epiendozoic, to 6 mm tall, caespitose, arising from spreading to penetrating branched filamentous systems, centrally coalesced into irregular pseudoparenchymatous discs or entangled fungiform masses, original spores not persistent; erect filaments sparsely to freely and irregularly to unilaterally branched, branches often ending in long multicellular hair-like projections, 3–4  $\mu\text{m}$  diam., 60–120  $\mu\text{m}$  long; cells of main axes cylindrical (6–)9–12(–20)  $\mu\text{m}$  diam., (8–)15–50 (–70)  $\mu\text{m}$  long, and only slightly tapering to tips, which are 7.5–10.0  $\mu\text{m}$  diam. where extensions not formed, each cell containing a single parietal lobate plastid with one pyrenoid; unicellular hairs unknown.

Monosporangia terminally clustered in groups of 3 or more on branched stalks or paired on 1–2 celled stalks adaxially on the lowermost cells of lateral branches, rarely single and scattered, ovoid, 7–13  $\mu\text{m}$  diam., 8–20  $\mu\text{m}$  long; tetrasporangia cruciate, paired on unicellular pedicels, solitary or in groups of 3, in similar positions to monosporangia, 13–22  $\mu\text{m}$  diam., 12–36  $\mu\text{m}$  long. Sexual plants unknown in the Carolinas.

**TYPE-LOCALITY.**—Bantry Bay, Ireland.

**HOLOTYPE.**—NMW.

**DISTRIBUTION.**—Nearly cosmopolitan. As yet, not known from South Carolina and Georgia.

**NORTH CAROLINA SPECIMENS STUDIED.**—Wrightsville Beach, Masonboro Inlet jetty, 18 Jan 1973, *Kapraun* (WNC). Wrightsville Beach, Masonboro Inlet jetty, Apr 1977, 6 Apr 1978, *Kapraun* (WNC; DUKE). Ft. Macon jetty, 30 Jun 1982, *Schneider 2831* (DUKE; US 88911; CWS).

**REMARKS.**—To date, known only from the shallow subtidal of Masonboro Inlet jetty, Wrightsville Beach, January and April, and the intertidal of Fort Macon jetty, June.

This is the first report of this taxon from North Carolina, although commonly known to the north (Woelkerling, 1973b). Only sporangiate plants have been found to date and these agree in all respects to recently published descriptions (Woelkerling, 1971, 1973b; Dixon and Irvine, 1977). Multicellular hair-like projections were found only in the January collection and tetrasporangia only in April.

### ***Audouinella densa* (Drew) Garbary**

FIGURE 2*d-i*

*Audouinella densa* (Drew) Garbary, 1979:490.

*Rhodochorton densum* Drew, 1928:168, pl. 38: figs. 17–24.

*Acrochaetium densum* (Drew) Papenfuss, 1945:308.—Stegenga and Vroman, 1976:276, figs. 1–9.

*Acrochaetium thuretii* sensu Kapraun, 1980:41, fig. 27. [Not *Acrochaetium thuretii* (Bornet) Collins and Hervey, 1917:98.]

*Acrochaetium hummii* Aziz, 1965:59, pl. 8: figs. 1–6, pl. 9: figs. 1–4, pl. 10: fig. 4 [nomen nudum].

**DESCRIPTION.**—Plants epiphytic or epizoid, 0.2–0.3(–0.5) mm tall, caespitose, arising from an irregularly branched prostrate system, often originally developed from a persistent septate spore, occasionally coalesced to form a pseudoparenchymatous disc, especially centrally, giving rise to several erect filaments, sparsely to much branched, irregular, alternate, opposite and secund, usually with a moderate branching above, the branches sometimes tapering toward the tips, often ending in colorless unicellular hairs; cells of the upright filaments cylindrical to clavate, 4–8



(–13)  $\mu\text{m}$  diam., 7–18  $\mu\text{m}$  long, each containing a single lobate to stellate plastid with a single pyrenoid.

Monosporangia single or 2–3 seriate, terminal, alternate secund, rarely opposite, sessile or on one-celled pedicels, single or in pairs, rarely clustered; monosporangia ovoid to ovoid-ellipsoid, 7–10  $\mu\text{m}$  diam., 10–13  $\mu\text{m}$  long.

TYPE-LOCALITY.—Fort Point, San Francisco, California, USA.

HOLOTYPE.—UC 294560 (*Gardner 4607*).

DISTRIBUTION.—Atlantic: North Carolina, South Carolina, Brazil, Netherlands. Pacific: Mexico, California, Japan, Kurile Islands.

NORTH CAROLINA SPECIMENS STUDIES.—Ft. Macon jetty, 27 Jun 1960, *Aziz* (DUKE 112). Beaufort, Radio Is. jetty, 15 Apr 1973, *Kapraun* (NCW). Wrightsville Beach, Masonboro Inlet jetty, 26 Feb 1978, 20 May 1978, 10 Sep 1978, *Kapraun* (NCW). Ft. Macon jetty, 1 Jul 1978, *Schneider 78-12-2* (DUKE; US 88913; CWS). Wrightsville Beach, Masonboro Inlet jetty, 4 Apr 81, *Searles* (DUKE, slide). Beaufort, Pivers Is., 7–8 Dec 1981, *Schneider 2760* (CWS). Beaufort, Radio Is. jetty, 21 Jun 1982, *Schneider 2790* (DUKE; US 88915; CWS). Ft. Macon jetty, 30 Jun 1982, *Schneider 2826* (DUKE; US 88912; CWS).

REMARKS.—Epiphytic on various algae and animals, in particular *Chaetomorpha aerea* (Dillwyn) Kützinger, throughout the year from the intertidal and shallow subtidal of Cape Lookout jetty, Fort Macon jetty and the Pivers Island seawall, Beaufort and Masonboro Inlet jetty at Wrightsville Beach. Also a single collection from 4.5 m in Port Royal Sound, South Carolina.

Germinating spores divide into two equal cells after attaching to a host (Figure 2*d,e*). One or both of these initials gives rise to an erect and/or prostrate filament, occasionally one initial remaining undivided for some time. The prostrate system consists of either irregular filamentous branched axes or becomes compacted into a pseudoparenchymatous disc (see Figure 2*f*).

This taxon was first reported from North Carolina in an unpublished thesis as "*Acrochaetium hummii*" (*Aziz*, 1965). *Stegenga* and *Vroman* (1976) recognized the *Aziz* plants as members of

a widespread heteromorphic acrochaetoid with seriate monosporangia tentatively identified by them as *Acrochaetium densum* (*Drew*) *Papenfuss* (= *Audouinella densa* [*Drew*] *Garbary*). In their report, *Stegenga* and *Vroman* (1976) call the report of gametangia in *A. hummii* by *Aziz* (1965) "strange." I could not find any sexual structures on *Aziz*'s specimens (slides); therefore, to date only monosporangiate plants are known from here. This is further evidence that the North Carolina specimens belong in the *A. densa* complex outlined by *Stegenga* and *Vroman* (1976). They suggest *A. microscopica* as a possible gametophytic generation if seriate monosporangia are not considered taxonomically important at the species level. Additional study is needed to clarify this relationship. For the present, I consider seriate monosporangia taxonomically significant, and leave the plants under the oldest validly published name, *A. densa*.

### *Audouinella hallandica* (Kylin) Woelkerling

*Audouinella hallandica* (Kylin) Woelkerling, 1973a:82, figs. 1–4.—*Schneider*, 1976:138.—*Searles* and *Schneider*, 1978:100.—*Kapraun*, 1980:41, figs. 18–20 [in part].  
*Chantransia hallandica* Kylin, 1906:123, fig. 8.  
*Acrochaetium dufourii* (Collins) *Børgesen*, 1915:19.—*Hoyt*, 1920:470, fig. 26.—*Taylor*, 1960:305.  
*Acrochaetium sargassi* *Børgesen*, 1915:17, figs. 7–10.—*Taylor*, 1960:306.

DESCRIPTION.—Plants epiphytic, to 1 mm tall, arising from an ovoid, obovate subglobose, disciform, elongated to rectangular basal spore; if disciform, the flared base of the spore to 20  $\mu\text{m}$ , otherwise 5–8  $\mu\text{m}$  diam. and the same size or slightly larger than cells of the filaments it produces; spore remaining simple producing 1–2(–3) erect filaments, branching irregularly lateral to secund, not closely set, beginning in the lowermost portions of the plant, occasionally tapering toward the apices, hairs unknown; lower cells cylindrical, 3–7  $\mu\text{m}$  diam., 10–30  $\mu\text{m}$  long, each containing a single parietal lobate plastid with one pyrenoid.

Monosporangia single or paired, lateral to se-



cund, more rarely terminal, sessile or on one-celled pedicels, obovate to ovoid, 5–10  $\mu\text{m}$  diam., 8–11(–16)  $\mu\text{m}$  long. Dioecious, spermatangia opposite on short lateral branches, rare; carpogonia sessile, rare.

TYPE-LOCALITY.—Hogardsgrund, Halland, Sweden.

HOLOTYPE.—LD (See Woelkerling, 1973a:84).

DISTRIBUTION.—North Carolina, South Carolina, Bermuda, Sargasso Sea, Florida to Venezuela, Brazil, Europe.

NORTH CAROLINA SPECIMENS STUDIED (representative).—Ft. Macon jetty, 13 Jul 1908, *Hoyt*, *Acrochaetium dufourii* (Collins) Hoyt (Isotype, DUKE 136). Beaufort, Pivers Is., 25 Jun 1960, *Aziz* (DUKE 113, 142). Beaufort, Shackleford jetty, 29 Jul 1961, *Aziz* (DUKE 143). Ft. Macon jetty, 5 Aug 1961, *Aziz* (DUKE 154–157). Beaufort, Shackleford jetty, 6 Aug 1961, *Aziz* (DUKE 144, 149–153). Beaufort, Shackleford jetty, 12 Aug 1962, *Aziz* (DUKE 145–147). Cape Lookout jetty, 8 Jun 1975, *Schneider* 947 (DUKE 15077, 15133; CWS). Onslow Bay, wreck, 9 Jun 1975, *Schneider* 998a (CWS). Wrightsville Beach, Masonboro Inlet jetty, 11 Nov 1977, *Kapraun* (WNC). Onslow Bay, reef, 11 Aug 1981, *Schneider* 2683 (CWS).

REMARKS.—Known as an epiphyte of *Dictyota* and *Sargassum* from shallow subtidal habitats near Beaufort and Wilmington, and on a variety of red and brown algae from deep water (to 35 m) environs, June–November.

This taxon is most easily recognized when attached to its host by the distinctive broad disc of cell-wall materials. The disc does not stain and the original spore remains as a simple elongated basal cell the same size or slightly larger than the cells of erect filaments it produces.

A recent study by Stegenga and Borsje (1977) demonstrates that a plant provisionally determined as *Audouinella hallandica* is the gametophyte of a heteromorphic plant whose sporophyte is tentatively determined as *Acrochaetium polyblastum* (Rosenvinge) Børgesen. No formal taxonomic changes for this species complex were offered, however.

## *Audouinella hoytii* (Collins), new combination

FIGURE 2j

*Acrochaetium hoytii* Collins, 1908:134.—Hoyt, 1920:470, figs. 27, 28.—Williams, 1948:690; 1951:153.—Searles and Schneider, 1978:100.—Wiseman, 1978:29.

DESCRIPTION.—Plants epiphytic, 0.2–1.3 mm tall, arising from a persistent, large, globose spore, 9–15(–28)  $\mu\text{m}$  diam. including an obvious wall 2–3  $\mu\text{m}$  thick; spore superficial to slightly embedded in host tissue, elongating to 30  $\mu\text{m}$ , being obviously broader than the cells it produces, remaining simple, rarely forming one or a few accessory cells, producing 1–2(–4) erect filaments; erect branching infrequent to frequent, often secund, ultimate branches elongated, tapering to the apices for the most part, 2–3  $\mu\text{m}$  diam., hairs unknown; cells of the main axes cylindrical, 5–7  $\mu\text{m}$  diam., 10–20  $\mu\text{m}$  long, each with a single parietal plastid and a large central pyrenoid.

Monosporangia secund or lateral on upper portions of the plant, sessile or on one-celled pedicels, oblong, 5.0–7.5  $\mu\text{m}$  diam., 11–15  $\mu\text{m}$  long. Monoecious, spermatangia lateral and terminal on short lateral branching systems; carpogonia sessile, lateral; carposporophytes developing as short branching systems lateral on main axes or near the base of branches, with 4–16 terminal carpospores, 4–9  $\mu\text{m}$  diam., 7.0–13.5  $\mu\text{m}$  long.

TYPE-LOCALITY.—Fort Macon jetty, vicinity Beaufort, North Carolina, USA.

HOLOTYPE.—US 33650.

DISTRIBUTION.—North Carolina, South Carolina.

NORTH CAROLINA SPECIMENS STUDIED.—Ft. Macon jetty, 20 Sep 1905, *Hoyt* (US 43499). Ft. Macon jetty, 12 Oct 1905, *Hoyt* (Holotype, US 33650). Ft. Macon jetty, 15 Aug 1906, *Hoyt* (DUKE 137; US 43500a, 33651). Beaufort harbor, 5 Oct 1906, *Hoyt* (DUKE 1460; US 43500b). Ft. Macon jetty, 13 Jul 1908, *Hoyt* (DUKE 1461; US 33652, 2803 as P.B.-A. 1540). Beaufort, Shackleford jetty, 14 Jul 1938, *Blomquist* (DUKE 133). Cape Lookout jetty, 28 Aug 1946, *Williams* (CWS). Ft. Fisher outcropping, July 1955, *Rho*



(DUKE 139). Beaufort, Shackleford jetty, 4 Jul 1960, *Aziz* (DUKE 119, 122, 123). Beaufort, Radio Is. jetty, 5 Jul 1960, *Aziz* (DUKE 148). Beaufort, Pivers Is., 18 Jul 1974, *Searles* (DUKE 16091). Beaufort, Radio Is. jetty, 13 Jun 1978, *Schneider* 78-4-5b (CWS). Beaufort, Duncan breakwater, 27 Jun 1978, *Schneider* 78-10-20 (CWS). Beaufort, Radio Is. jetty, 20 Sep 1981, *Schneider* 2738 (DUKE 16522; US 88914; CWS). Beaufort, Radio Is. jetty, 21 Jun 1982, *Schneider* 2789 (DUKE; US 88915; CWS). Beaufort, Radio Is. jetty, 20 Jul 1982, *Schneider* 2861 (DUKE; US 88916; CWS).

REMARKS.—Known as an epiphyte of *Dictyota*, *Padina*, and other seaweeds from shallow subtidal habitats in the Beaufort area, June–October.

Although similar in morphology to *Audouinella alariae* (Jonsson) Woelkerling (1973b) from New England and Europe, main axes, carposporangia, and monosporangia of *A. hoytii* are one-half the size of the first mentioned taxon. A further comparison is necessary to clarify the relationship of these two species. *Audouinella hoytii* has also been linked to *A. pectinata* (Kyllin) Papenfuss by Woelkerling (1971).

### *Audouinella hypneae* (Børgesen), new combination

FIGURE 2*k-l*

*Chantransia hypneae* Børgesen, 1909:2, fig. 2.

*Acrochaetium hypneae* (Børgesen) Børgesen, 1915:51, figs. 53, 54.

*Acrochaetium seriatum* Børgesen, 1915:32, figs. 25–28.—Williams, 1948:690—Searles and Schneider, 1978:100.

DESCRIPTION.—Plants epiphytic or epiendo-phytic to 1 mm tall arising from small compact to spreading filamentous prostrate system composed of one or more irregularly bent, branched filaments that can be coalesced centrally into a pseudoparenchymatous disc; each cell of the disc or ramified filaments capable of producing an erect filament; erect branches little to radially and much branched below, alternate, often pectinate secund above, cells cylindrical, 6–10  $\mu$ m diam., 16–22  $\mu$ m long below, tapering to 4–7  $\mu$ m diam., 16–30  $\mu$ m long in the ultimate segments,

each containing a single parietal plastid with an obvious pyrenoid, occasionally bearing unicellular hyaline hairs to 60  $\mu$ m long.

Monosporangia single, rarely paired, lateral in long second series or rarely terminal, occasionally scattered, sessile or on one-celled pedicels, oblong-ovoid, 6–10  $\mu$ m diam., 9–13  $\mu$ m long. Gametangia unknown.

TYPE-LOCALITY.—St. Thomas, Virgin Islands.

HOLOTYPE.—C.

DISTRIBUTION.—North Carolina, South Carolina, Georgia, Bermuda, Florida, Virgin Islands, Brazil, East Indies.

NORTH CAROLINA SPECIMENS STUDIES.—Ft. Macon jetty, 15 Jul 1907, *Hoyt* (US 42553). Cape Lookout jetty, 28 Sep 1946, *Williams* (CWS). Beaufort, Shackleford jetty, 4 Jul 1960, *Aziz* (DUKE 124). Cape Lookout jetty, 8 Aug 1961, *Aziz* (DUKE 186–187). Onslow Bay, reef, 11 Jul 1976, *Searles* (CWS). Onslow Bay, reef, 15 Jul 1981, *Handsel*, *BLM* 65818144, 65818145, 65818148 (Duke Marine Lab Reference Museum). Onslow Bay, reef, 28 Jul 1981, *Amsler*, *BLM* 65818152 (Duke Marine Lab Reference Museum). Onslow Bay, reef, 11 Aug 1981, *Schneider* 2712 (DUKE 16523; CWS). Cape Lookout jetty, 5 Jul 1982, *Schneider* 2841 (DUKE; US 88917; CWS).

REMARKS.—On a variety of plant and animal hosts from Beaufort area jetties and on *Arthrocladia*, *Spatoglossum*, and other hosts from deep offshore, July–September.

North Carolina plants show variation in their attachment, ranging from the small compact, epiphytic disc illustrated for *Acrochaetium seriatum* (Børgesen, 1915:32) to the short branched or simple prostrate epiphytic (*A. gracile*, Børgesen, 1915:26) or endophytic (*A. hypneae*, Børgesen, 1915:52) filament. In his discussion of *A. hypneae*, Børgesen (1915:52) states, "If the basal part is left out of consideration it cannot be denied that the above, [newly] described *Acrochaetium seriatum* shows great likeness to this species. But while the present plant has an endophytic base the other is epiphytic." I have observed epiphytic, epi-endo-phytic and endophytic bases of this small spored



acrochaetoid on the same host, *Arthrocladia*, from 30 m offshore. Basal system variation has previously been used as a taxonomic criterion, even though this variation may have been due to the texture of the host. Recent studies have shown great variation within the attachment morphology for *Audouinella daviesii* (Dillwyn) Woelkerling, and other species (Woelkerling 1971, 1973b). I therefore propose that plants previously reported from North Carolina as *Acrochaetium seriatum* Børgesen by Williams (1948) are the same as those I have observed.

Because the single criterion that separates them appears unreliable, *Acrochaetium seriatum* is synonymized under the earliest available taxon, *Audouinella hypneae*. A recent report of somewhat larger spore dimensions for *A. seriatum* than shown in this and classical reports requires additional study. If the plants reported by Hall and Eiseman (1981) conform to Børgesen's *A. seriatum*, then spore size distinction between *A. hypneae* and *A. saviana* is clouded, and further taxonomic reductions may be necessary. Until additional studies are completed, the key and description of *A. hypneae* in this report conform to Carolina specimens and classical reports (e.g., Børgesen, 1915; Taylor, 1960).

It is, at this stage, still possible to segregate *Audouinella bispora* from *A. hypneae* on the basis of size and type of sporangia. I expect however, as did Børgesen, that these two taxa are one and that further collections and life history studies will bear this out. The necessity of a taxonomic study of the many Børgesen Caribbean acrochaetoid species is obvious to me. Several of the small spored, partially or wholly endophytic or epiphytic plants will no doubt prove to be conspecific. At present, I consider the evidence sufficient to synonymize two of the species in this complex.

### *Audouinella infestans* (Howe and Hoyt) Dixon

FIGURE 2m

*Audouinella infestans* (Howe and Hoyt) Dixon in Parke and Dixon, 1976:590.

*Acrochaetium infestans* Howe and Hoyt, 1916:116, pl. 14.—Hoyt, 1920:473, pl. 68.

*Kylinia infestans* (Howe and Hoyt) Papenfuss, 1947:438.—Taylor, 1960:301.

*Colaconema infestans* (Howe and Hoyt) Woelkerling, 1973a:89, figs. 5, 6.—Searles and Schneider, 1978:100.

**DESCRIPTION.**—Plants endophytic or endozoic with emergent axes to 100  $\mu\text{m}$  tall exclusive of hairs, internal axes consisting of tortuous, serpentine, or labyrinthine irregularly branched filaments, sparse and straight for considerable distances, often crowded between host cells or compacted and subparenchymatous, cells irregular to elongate, (2–)4–8(–13)  $\mu\text{m}$  diam., 6–60  $\mu\text{m}$  long; emergent axes to 10 or more cells high but generally less, simple or sparingly and irregularly branched, occasionally bearing terminal hairs to 170  $\mu\text{m}$  long; cells cylindrical to ellipsoid, 3–7  $\mu\text{m}$  diam., 6–30  $\mu\text{m}$  long, containing a single parietal lobate plastid with a single pyrenoid.

Monosporangia single or paired, terminal or lateral, often on the adaxial surface, sessile or on one celled pedicels, ovoid to ellipsoid, 4–6(–9)  $\mu\text{m}$  diam., 6–15  $\mu\text{m}$  long. Gametangia unknown.

**TYPE-LOCALITY.**—Onslow Bay, North Carolina, USA.

**HOLOTYPE.**—US 56009.

**DISTRIBUTION.**—North Carolina, Bermuda, Sargasso Sea, British Isles, Mediterranean, Japan.

**NORTH CAROLINA SPECIMENS STUDIES.**—Onslow Bay, reef, 11 Aug 1914, *Radcliffe*, (Holotype, US 56009, Isotypes, US 33514, 33653, 336534, DUKE 140). Cape Lookout jetty, 8 Aug 1961, *Aziz* (DUKE, slide). Onslow Bay, wreck, 8 Jul 1976, *Searles* (CWS). Beaufort, Radio Is. jetty, 13 Jun 1978, *Schneider 78-4-5a* (CWS). Onslow Bay, reef, 15 Jul 1981, *Searles BLM 65818144* (Duke Marine Lab Reference Museum). Onslow Bay, reef, 28 Jul 1981, *Amsler BLM 65818152* (Duke Marine Lab Reference Museum).

**REMARKS.**—Collections on various hydroids, *Dictyota*, and *Sargassum* from deep offshore habitats and shallow subtidal habitats near Beaufort and Wilmington, June–August.

### *Audouinella microscopica* (Nägeli) Woelkerling

*Audouinella microscopica* (Nägeli) Woelkerling, 1971:33, figs. 10, 23A.—Searles and Schneider, 1978:100.—Kapraun, 1980:41, figs. 21, 22.

*Callithamnion microscopicum* Nägeli in Kützinger, 1849:640.



*Acrochaetium trifilum* (Biffham) Batters, 1902:58.

*Acrochaetium parvulum* (Kylin) Hoyt, 1920:470, fig. 25.

*Acrochaetium compactum* Jao, 1936:241, pl. 10: figs. 6–14.—Williams, 1948:690.

*Kylinia crassipes* (Børgesen) Kylin, 1944:13.—Taylor, 1960:300.

**DESCRIPTION.**—Plants minute epiphytes, 20–150(–220)  $\mu\text{m}$  tall exclusive of hairs, arising from a persistent subglobose, isodiametric, to cylindrical spore with or without a thick cell wall, 5–15  $\mu\text{m}$  diam., close to the same size as the cells it produces; spore giving rise to 1–6 erect and/or lateral filaments, commonly arcuate, simple to much branched, secund, irregular or opposite, branches short, tapering; cells barrel-shaped, isodiametric to cylindrical, 3–10  $\mu\text{m}$  diam., 3–11  $\mu\text{m}$  long, having a single lobate to stellate plastid with one pyrenoid, often bearing hyaline hairs to 50  $\mu\text{m}$  long.

Monosporangia terminal and secund to opposite, sessile or on one-celled pedicels, ovoid, 4–10(–15)  $\mu\text{m}$  diam., 6–15(–22)  $\mu\text{m}$  long.

**TYPE-LOCALITY.**—Torquay, England.

**HOLOTYPE.**—L 940285 . . . 306.

**DISTRIBUTION.**—Almost cosmopolitan in distribution.

**NORTH CAROLINA SPECIMENS STUDIED.**—Beaufort Inlet, sea buoy, 27 Jul 1909, *Hoyt* (DUKE 141; US 33655). Beaufort, Shackleford jetty, 29 Nov 1940, *Blomquist 11472* (DUKE 676, as *Callithamnion polyspermum*). Ft. Macon jetty, 27 Feb 1971, *Schneider 50A* (CWS). Wrightsville Beach, Masonboro Inlet jetty, 9 Jun 1977, *Kapraun* (WNC). Beaufort, Radio Is. jetty, 20 Jul 1982, *Schneider 2865* (CWS).

**REMARKS.**—Known as an epiphyte on a variety of intertidal and shallow subtidal seaweeds from the Beaufort and Wilmington areas, throughout the year. Tetrasporangia have not been observed on North Carolina specimens and only rarely elsewhere (Woelkerling, 1972).

Although some authors have chosen to retain the similar *Audouinella microscopica* and *A. parvula* (Kylin) Dixon as separate entities (e.g., Dixon and Irvine, 1977), the grounds for their separation seem unclear and unsubstantial in light of the morphological diversity shown for the *A. microscopica* complex based upon studies of several type

collections (Woelkerling, 1972). Stegenga and Mulder (1979), however, find some of the members of this complex synonymized by Woelkerling (1972) belong in the separate genera based upon their utilization of a multiple generic scheme for the family. There is, however, no doubt that all previously and recently collected Carolina specimens easily fit into the circumscription of *A. microscopica* proposed by Woelkerling (1971, 1972, 1973b), which for the present I continue to follow. Examination of type material of *A. parvula* (Kylin, 1906 as *Chantransia parvula*) is still necessary if a formal transfer is to be made.

*Audouinella microscopica* is reported as *Acrochaetium trifilum* (Biffham) Batters for adjacent Virginia (Humm, 1979). That listing follows Aziz (1965), which finds *A. parvulum* synonymous with several Caribbean taxa, of which *A. trifilum* is the oldest available binomial. The synonyms included *A. compactum* Jao and *A. crassipes* (Børgesen) Børgesen, both of which also appear as synonyms of *A. microscopica* (Woelkerling, 1972). Aziz did not mention *A. microscopica* in his paper, and at that time it was not listed for the Southeast or Caribbean (Taylor, 1960), but it is clear that the two are the same, with *A. microscopica* having historical precedence over *A. trifilum*. I therefore reject usage of the latter name.

### *Audouinella ophioglossa*, new species

FIGURE 3

Plantae epiendophyticae, 1.0–2.2 mm elatae, spora persistenti magna globosa exorientes, 7.5–12.5  $\mu\text{m}$  diametro; spora basalis filum singulare unramosum aut ramosum furcatum irregulare contortum producens qui hospitem cum cellulas 2–4  $\mu\text{m}$  diametris profunde penetrans, vel basem unicellulam remanens; spora basalis 1–2 axes erectas ramosas producens, secundas ad alternas et oppositas, rami plures communes super; cellulae filorum erectorum cylindricae, 4–5  $\mu\text{m}$  diametris, 45–55  $\mu\text{m}$  longae segmentis infernis, cellula omnis plastum singularem lobatum ad spiralem parietalem cum pyrenoide singulari inconspicua capiens; trichomata unicellularia terminalia vel lateralialia, ad 2 mm, saepe cum ramis gametangiis consociata.



Monosporangia terminalia in ramis brevibus aut lateralibus, secunda ad alterna aut opposita, sessilia aut in pedicellis unicellularis, singularia vel binata, ovoidea ad ellipsoidea, 6.0–12.5  $\mu\text{m}$  diametris, 12.5–20.0  $\mu\text{m}$  longa, plerumque cum gametangiis consociata. Plantae monoeciae, rami spermatangiis quadriverticillati, oppositi vel minus plerumque ramus unicus ad uterque nodum in seriebus longis in partibus superis plantae; spermatangia binata in pedicellis unicellulis, globosa, 2.5  $\mu\text{m}$  diametris; carpogonia lateralibus, opposita vel juxta monosporangium, aliquando in verticillo ramorum spermatangiorum facientia, non nisi unum carposporophytum ad uterque nodum producentia, saepe in seriebus longis interruptis; carposporangia terminalia globosa, 10–15  $\mu\text{m}$  diametris.

Specimen holotypicum a SCUBA lectum, 20 VII 1973, 34°23.0'N, 76°36.0'W (North Carolina), in profunditate 22 metrorum, in *Dudresnaya crassa* Howe, leg. R.B. Searles, in herbariis Universitatis Dukensis, No. 16585, ♀♂; Isotypi DUKE, US 88918.

DESCRIPTION.—Plants epiendophytic, 1.0–2.2 mm tall, arising from a persistent, large, globose spore, 7.5–12.5  $\mu\text{m}$  diam., which produces a single unbranched or forked branched irregularly contorted filament that deeply penetrates host tissue with cells 2–4  $\mu\text{m}$  diam., or remains as a unicellular base; basal spore giving rise to 1–2 erect branched axes, secund to alternate and opposite, more common above; cells of the erect filaments cylindrical, 4–5  $\mu\text{m}$  diam., 45–55  $\mu\text{m}$  long in lower segments; each cell containing a single lobate to spiral parietal plastid with a single inconspicuous pyrenoid, unicellular hairs terminal or lateral, to 2 mm, often associated with gametangial branches.

Monosporangia terminal on short branches or lateral, secund to alternate or opposite, sessile or on one-celled pedicels, single or in pairs, ovoid to ellipsoid, 6.0–12.5  $\mu\text{m}$  diam., 12.5–20.0  $\mu\text{m}$  long, commonly associated with gametangia. Monoecious, spermatangial branches in a whorl of 4, opposite paired or less commonly one per node, in long series in the upper parts of the plant;

spermatangia paired on one-celled pedicels, globose, 2.5  $\mu\text{m}$  diam.; carpogonia lateral, opposite or adjacent to a monosporangium, occasionally forming in a whorl of spermatangial branches, producing only one carposporophyte per node, often in a long interrupted series; carposporangia terminal, globose, 10–15  $\mu\text{m}$  diam.

TYPE-LOCALITY.—Onslow Bay, North Carolina, USA.

HOLOTYPE.—DUKE 16585.

DISTRIBUTION.—Endemic to North Carolina as far as currently known.

NORTH CAROLINA SPECIMENS STUDIED.—Onslow Bay, reef, 18 Sep 1972, *Schneider 553e* (CWS). Onslow Bay, reef, 19 Jul 1973, *Schneider 665a* (CWS). Onslow Bay, reef, 20 Jul 1973, *Searles* (Holotype, DUKE 16585; Isotypes, DUKE 16586, 16587, US 88918). Onslow Bay, reef, 20 Jul 1973, *Schneider 716a* (Topotypes, CWS). Onslow Bay, reef, 19 Jun 1980, *Searles* (DUKE 16589).

REMARKS.—*Audouinella ophioglossa* is known 22–35 m offshore on *Dudresnaya crassa*, June–September. The species is named for the general appearance of the basal spore and often forked endophytic filament, which resembles the head of a snake with extended tongue (see Figure 3*b–d*). Of the several species worldwide with a persistent, obvious basal spore which produces a deep penetrating endophytic filament, this newly described plant is most similar to *Audouinella subtilissima* (Kützinger) Garbary, an epiendophyte of *Dudresnaya* and other species along the French coast. The new taxon, *A. ophioglossa*, differs from *A. subtilissima* in that its branches do not taper toward the tips, in having blunt apices, a smaller filament diameter (4–5 vs. 6–7  $\mu\text{m}$ ), and conspicuous unicellular hairs (see Figure 3*f,h,j*). Hamel (1928a) reports *A. subtilissima* as having some filaments end in pseudohairs that do not appear to be unicellular, a feature not illustrated by him or by Kützinger (1861). Hamel (1928a) describes and illustrates other characters of *A. subtilissima* that vary from the North Carolina plant: oval to oblong carposporangia, carpogonia often distal to spermatangia on the same branch, and laterally disposed spermatangial branches. In *A. ophiog-*



*lossa*, the carpogonia are either proximal to spermatangial branches (Figure 3f), paired with one (Figure 3i), or are found as one branch in a whorl of 4, the remainder being male axes (Figure 3h). The verticillate arrangement of male branches in the new taxon (Figure 3h,j) is unique for this species cluster of *Audouinella*. In *A. ophioglossa*, monosporangia, male branches or carpogonia are commonly oppositely arranged (Figure 3f,l,m), or a carpogonium is disposed opposite to a monosporangium (Figure 3f). Opposite spermatangia are found occasionally in *Acrochaetium kuckuckianum* Hamel (1928b), which has a similar mode of attachment to *A. ophioglossa*. Its size and dioecious habit still separate it clearly from the new species.

From *Audouinella corymbifera*, the only other member from North Carolina having a persistent spore with a penetrating endophytic filament, *A. ophioglossa*, is distinguished by a smaller basal spore, narrower erect filaments, its monoecious habit and the disposition of spermatangial branches.

### ***Audouinella saviana* (Meneghini) Woelkerling**

*Audouinella saviana* (Meneghini) Woelkerling 1973b:560, figs. 56–60.—Schneider, 1976:138.—Searles and Schneider, 1978:100.

*Callithamnion savianum* Meneghini, 1840:511.

*Acrochaetium thuretii* (Bornet) Collins and Hervey, 1917:98.

*Audouinella thuretii* (Bornet) Woelkerling, 1971:36, figs. 12, 24.

[Not *Audouinella thuretii* sensu Kapraun, 1980:41.]

**DESCRIPTION.**—Plants epiphytic to epiendophytic, to 4 mm tall, arising from a compact, mostly superficial prostrate system of short, simple or branched filaments, free from each other to coalesced into an irregular pseudoparenchymatous disc, the original spore not recognizable; prostrate filaments the same size or distinctly larger than erect ones; erect filaments with irregular or alternate to secund branching, cells of main axes and branches cylindrical 7–14  $\mu$ m diam., 20–60  $\mu$ m long, sometimes 4–6  $\mu$ m diam. in the ultimate branches, unicellular hairs absent or rare, each cell containing a single parietal lobate plastid.

Monosporangia single or paired, adaxially secund to irregularly arranged, sessile or on 1 (or 2) celled elongate pedicels, ovoid to ellipsoid, 10–15  $\mu$ m diam., 18–27  $\mu$ m long. Tetrasporangia cruciate, with shape and positions similar to monosporangia, often borne simultaneously, 17–24  $\mu$ m diam., 26–34  $\mu$ m long. Monoecious, spermatangia sparse, on short branchlets near the base of branches; carpogonia sparse and solitary on lower segments near the base of branches, carpospores 9–13  $\mu$ m diam., 18–21  $\mu$ m long.

**TYPE-LOCALITY.**—Genoa, Italy.

**HOLOTYPE.**—FL.

**DISTRIBUTION.**—Atlantic North America, Bermuda, Caribbean, Atlantic Europe, Mediterranean, Juan Fernandez Islands, Australia, California.

**NORTH CAROLINA SPECIMENS STUDIED** (representative).—Beaufort, Duncan Breakwater, 19 Oct 1940, *Blomquist 11447A* (DUKE 134, 1459), Ft. Macon jetty, 27 Jun 1960, *Aziz* (DUKE 114, 116, 159). Marshallberg, Cowper Is., 29 Aug 1962, *Wirtensen* (DUKE 115). Beaufort, Bird Shoals, 10 Jun 1971, *Brauner* (DUKE 12459). Wrightsville Beach, Figure 8 Is., Jun 1972, *Kapraun* (NCW). Onslow Bay, reef, 9 Jun 1974, *Schneider 904* (DUKE 13514; CWS). Beaufort, Radio Is. jetty, 13 Jun 1978, *Schneider 78-4-17* (CWS). Onslow Bay, wreck, 18 Jun 1978, *Schneider 78-6-9* (DUKE 16271; CWS). Beaufort, Radio Is. jetty, 14 Sep 1981, *Schneider 2727* (CWS). Cape Lookout jetty, 5 Jul 1982, *Schneider 2852* (CWS).

**REMARKS.**—Epiphytic usually on *Codium* but also known on *Dictyopteris* and other coarse algae from shallow subtidal and deep offshore habitats to 30 m, May–October.

Dixon and Irvine (1977) and Garbary (1979) question the conspecificity of *Audouinella thuretii* (Bornet) Woelkerling with *A. saviana* as proposed by Woelkerling (1973b). In a numerical taxonomic approach to the Acrochaetiaceae, Garbary (1979) finds dissimilarity in some published descriptions of *A. thuretii* and *A. saviana* and states "that [Woelkerling's] conclusions are so different from those reached by other workers is perhaps a reflection of the limitations of dealing with her-



barium specimens of acrochaetioid algae." I reject the inference that taxa can be distinguished on the basis of written description alone, especially if these are not type descriptions, as is often the case in Garbary's (1979) report. Therefore, I continue to follow the results of Woelkerling (1973b) who, using herbarium specimens, found type material of the two taxa conspecific, and accept *A. saviana* as the epithet for North Carolina plants. This taxon may be an alternate generation of *A. dasyae* (see prior discussion and Stegenga and Borsje, 1976).

Although I have not found unicellular hairs on specimens from the Carolinas, in conformity with those from New England (Woelkerling, 1973b), Hall and Eiseman (1981) reported them on plants during the winter months in Florida.

### *Audouinella secundata* (Lyngbye) Dixon

*Audouinella secundata* (Lyngbye) Dixon in Parke and Dixon, 1976:590.—Kapaun, 1980:41, figs. 23–25.

*Callithamnion daviesii* var. *secundatum* Lyngbye, 1819:129, pl. 41: figs. B4–B6.

*Colaconema secundata* (Lyngbye) Woelkerling, 1973a:94, figs. 7, 8.—Searles and Schneider, 1978:100.

*Acrochaetium virgatulum* (Harvey) Bornet, 1904:xxii.—Williams, 1948:690; 1951:153.

*Kylinia virgatula* (Harvey) Papenfuss, 1947:437.—Taylor, 1962:214.

**DESCRIPTION.**—Plants epiphytic or epizoic, to 3 mm tall, scattered to caespitose, arising from a uni- to bistratose, generally compact pseudoparenchymatous disc, the original spore not persistent; disc giving rise to several erect, usually freely and irregularly branched with laterals often consisting of only 1–5 cells, with or without lateral and terminal unicellular hairs to 300  $\mu$ m long;

cells of main axes cylindrical 8–15(–20)  $\mu$ m diam., 15–100  $\mu$ m long, each with an axial or parietal stellate plastid and single central pyrenoid.

Monosporangia lateral or terminal on shorter lateral branches, sessile or pedicellate, single, paired or rarely in groups of 3, ovoid, (6–)10–20  $\mu$ m diam., (10–)15–26(–32)  $\mu$ m long.

**TYPE-LOCALITY.**—Kvívig, Faeroes Islands.

**HOLOTYPE.**—C.

**DISTRIBUTION.**—Atlantic coast of North America (not reported from Georgia), Sargasso Sea, Europe, Mediterranean, Canary Islands, Australia.

**NORTH CAROLINA SPECIMENS STUDIED.**—Beaufort, Pivers Is., 10 Aug 1907, *Hoyt* (DUKE 188 D; US 71721a,b). Beaufort, Shackleford jetty, 12 Aug 1907, *Hoyt* (US 71721c). Ft. Macon jetty, 15 Apr 1909, *Hoyt* (DUKE 188A; US 33656). Beaufort, Shackleford jetty, 19 Jun 1960, *Aziz* (DUKE 126, 131, 132). Beaufort, Bird Shoals, 10 Jun 1971, *Brauner* (DUKE 12457, 12459). Beaufort, Bird Shoals, 20 Jun 1971, *Brauner* (DUKE 12480).

**REMARKS.**—Epiphytic on a variety of algae intertidally, April–August.

Although some authors maintain a specific distinction between *Audouinella secundata* and *A. virgatula* (Harvey) Dixon (e.g., Dixon and Irvine, 1977; Kornmann and Sahling, 1978), I have observed morphological plasticity in North Carolina plants that corroborates the findings leading to the recent synonymy of the two taxa (Woelkerling, 1973a, 1973b).

Easiest to distinguish in young stages, the prostrate system develops from an orbicular, parenchymatous group of cells. This disc may later proliferate as prostrate filamentous axes, obscuring the central disc and becoming more similar to later stages of *Audouinella dasyae* and *A. saviana*.



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FIGURE 1.—*Audouinella affinis*: *a*, surface view of a basal spore with a single erect filament; *b*, transverse section of *Dictyota* cells displaced by the penetrating spore. *A. bispora*: *c*, epiphytic and endophytic (broken lines) attachment filaments; *d*, bisporangia in various stages of development; *e,f*, monosporangia. *A. botryocarpa*: *g*, detail of two cells showing lobate parietal plastids and associated multiple pyrenoids (clear); *h,i*, tetrasporangia; *j*, branch bearing monosporangia (some spent) and a single tetrasporangium; *k,l*, monosporangia. *A. dasyae*: *m,n*, axis rising on oblique angle from two-celled basal system; *o*, basal cells immersed in cell wall of *Ceramium*; *p*, maturing basal system with original panduriform basal cell still obvious.

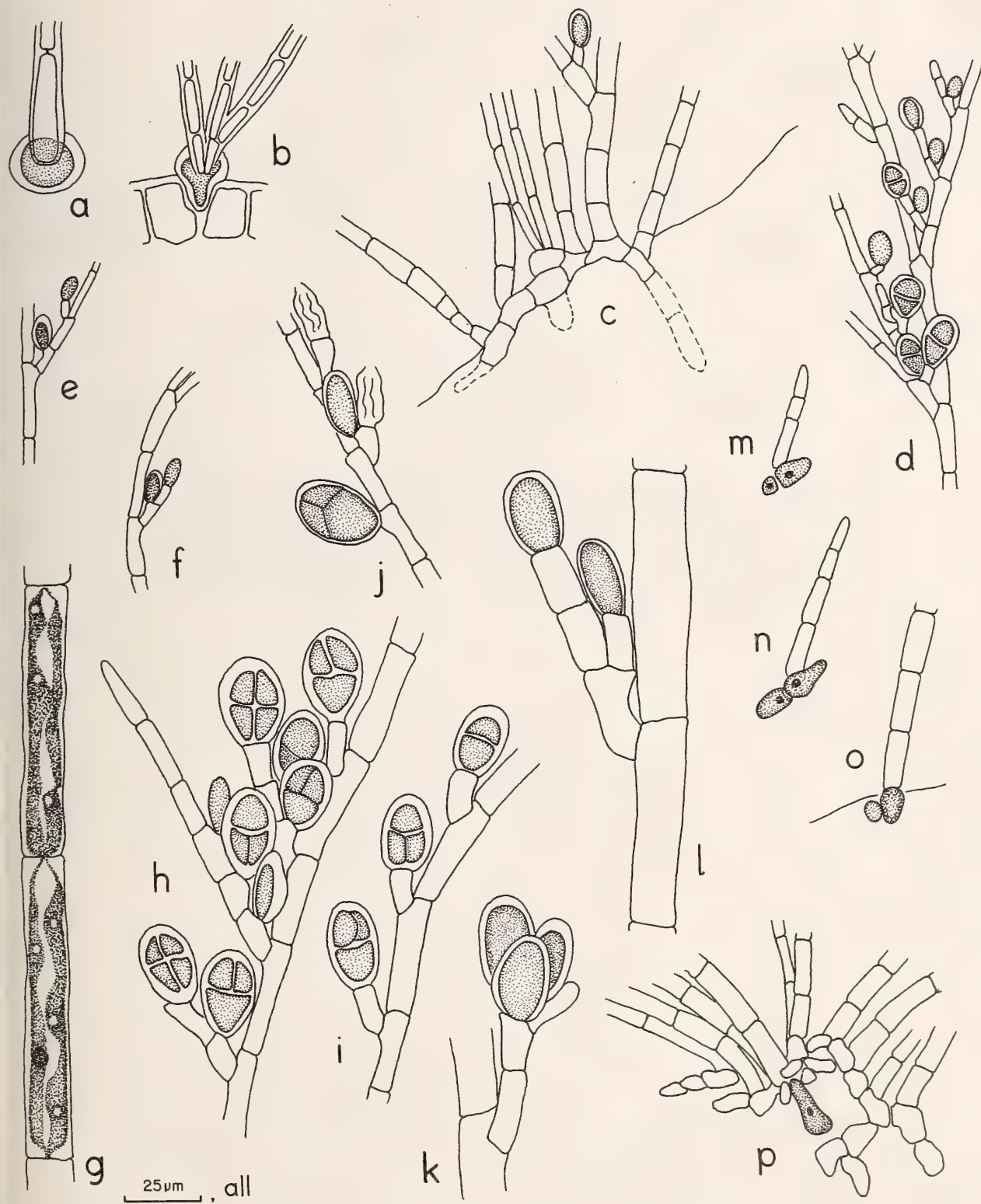




FIGURE 2.—*Audouinella daviesii*: *a-c*, various arrangements of monosporangia. *A. densa*: *d, e*, early prostrate system showing septate spore; *f*, habit on *Chaetomorpha*, single and seriate monosporangia; *g-i*, single and 2-3 seriate monosporangia. *A. hoytii*: *j*, habit of a monosporangiate plant, showing obvious persistent basal spore. *A. hypneae*: *k*, basal system with erect filaments; *l*, monosporangia in series. *A. infestans*: *m*, endophytic system and emergent axis with monosporangia and a single unicellular hair.

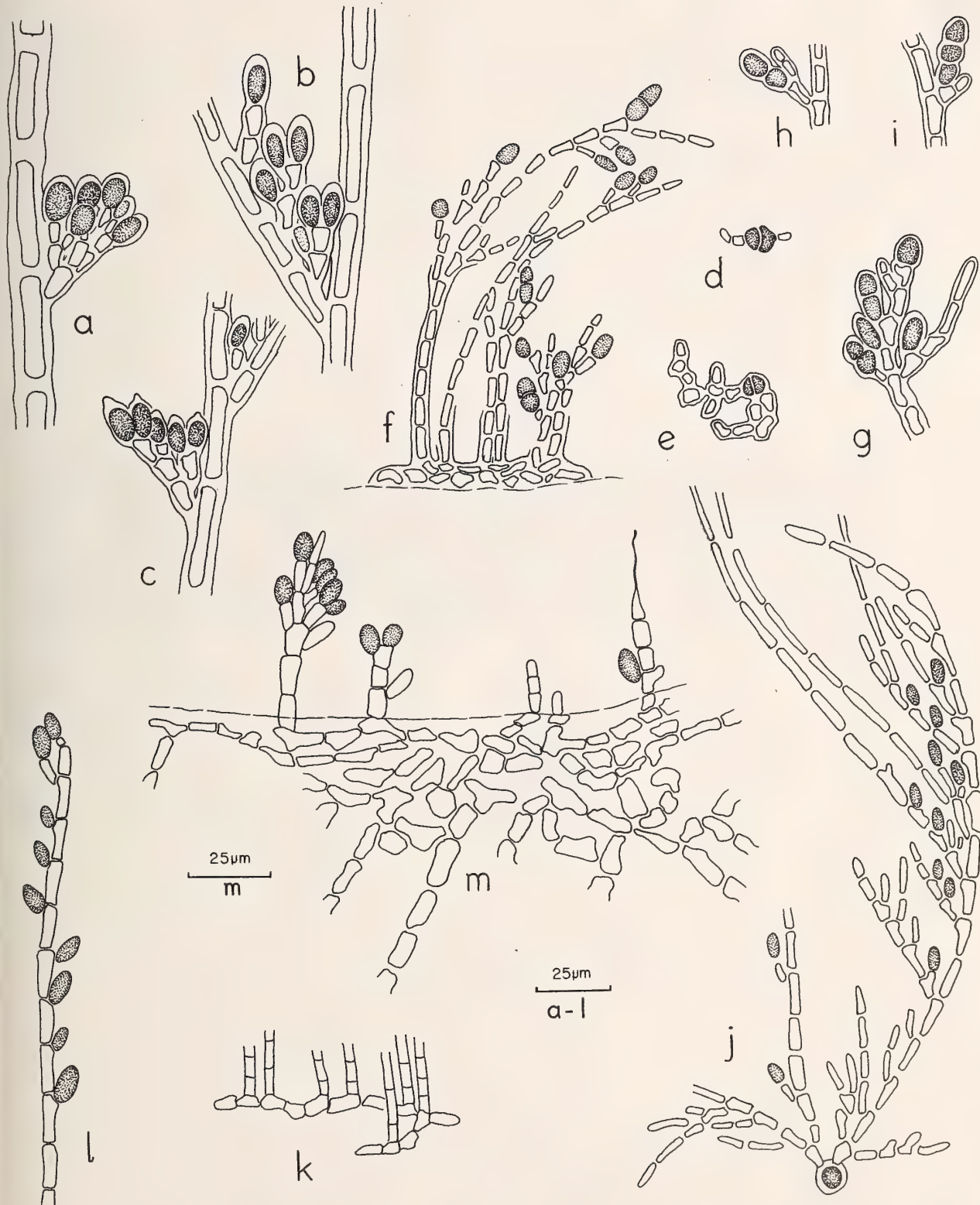
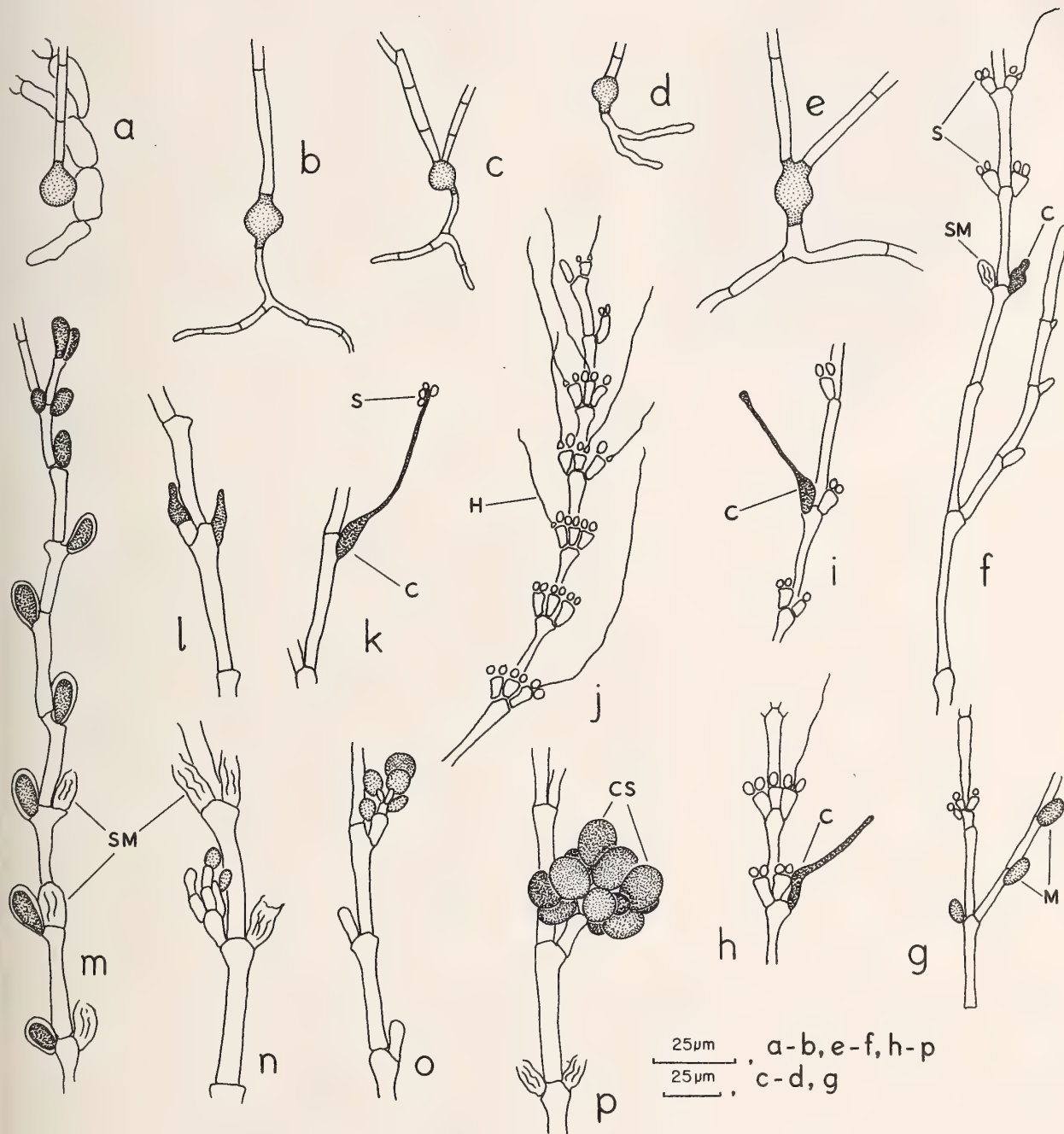




FIGURE 3.—*Audouinella ophioglossa*, new species: *a*, basal spore, without endophytic penetrating filament, adjacent to *Dudresnaya* cortical cells; *b-e*, basal spores with erect and forked penetrating filaments; *f*, habit, showing paired spermatangia (*s*) and a spent monosporangium (*sm*) opposite to a carpogonium (*c*); *g*, monosporangia (*m*) and a whorl of spermatangia; *h,i*, primarily male axis bearing carpogonia (*c*) with extended trichogynes, hair cell present; *j*, male axis with numerous unicellular hairs (*h*) among whorls of spermatangia; *k*, carpogonium with 4 spermatangia on trichogyne; *l*, opposite carpogonia; *m*, opposite or single monosporangia, some spent (*sm*); *n-p*, development of carposporophyte with carpospores (*cs*).







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